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# THE BRYOLOGIST

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## A SHORT HISTORY OF LICHENOLOGY<sup>1</sup>

CHARLES C. PLITT

Like the history of most things biological, the history of Lichenology, especially that most worth while, does not date very far back. Due to their little economic value, (especially true of the vast majority of Lichens, and particularly true for those found in the more habitable regions of the world) Lichens had hardly been thought worth while studying. Even Linnaeus dubbed them the "rustici pauperrimi" of vegetation, which has been quite properly translated. the "poor trash" of vegetation.<sup>2</sup> Linnaeus, however, was no particular friend of the Cryptogams, and the Lichens, in particular, received very little of his attention.

As to the derivation and meaning of the word "lichen," there are differences of opinion. According to Lindsay (History of British Lichens), it is derived from λειχήν—a wart, in allusion to the resemblance of the apothecia of many of the species to a wart. On the other hand Dillen is quoted as stating that the word is derived either from λειχῶ—Latin *lingo*, to lick up, because the plants can absorb water so readily, or from λειχήν, because of the efficacy of these plants in curing the disease known as λειχήν.

The word λειχήν appears in Dioscorides, later also in Pliny, but it is not definitely understood what plant is meant; some think that some *Marchantia* form of Liverwort is meant, and no Lichen; Krempelhuber (Geschichte der Lichenologie), however, says that there is no more reason for supposing this, than that a Lichen is what is meant.

Several Lichens were no doubt known to the ancients—*Usnea dasypoga*, for example, seems to have been known to Aristotle—likewise several furnishing valuable purple dyes are alluded to under various names in Dioscorides, Theo-

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<sup>1</sup>This paper was read at a biological seminary meeting about three years ago. It is here presented, as it was also on the above occasion, for the benefit of such readers who, although interested, in a general way, in Lichens, may not be so much so as to find the time to read, or, perhaps, may not have access to the works treating this subject more elaborately; at the same time, it is hoped that some will have their interests aroused to the study of this most interesting class of plants.

<sup>2</sup>Schneider, "Guide to the Study of Lichens," p. 6, or Schneider, "A Text book of General Lichenology," p. 8. Both of these books are recommended for those interested in the history of Lichens.

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phrastus, and Pliny. However, as a class of plants they did not attract much scientific attention, nor did they become the subject of special classification until about the beginning of the 18th century.

The ideas of earlier authors concerning them, of course, were very primitive and erroneous. Some believed them excrementitious matter produced by the earth, the rocks or the trees. Some believed that depending upon external media Lichens, Algae, or Fungi might arise, and even animalcules. Another form of belief was that they were merely the result of the decomposition of higher vegetation. Sprengel speaks of the Lichens as formed of nothing but the vegetable juices, and except here and there, some slight rudiments of a cellulose organization.

Up to the time of Tournefort, 1694, only such forms as were remarkable for their size, their color, or their supposed medicinal virtues received any attention.

The abstraction of a purple dye from certain species of Lichens dates far back into history, and must have been quite a profitable industry—to-day, however, it is limited to the abstraction of litmus, cudbear, and orchil.

As to their medicinal virtues; it is not surprising that, at a time when people believed in the "doctrine of signatures"—that is, that a plant had stamped upon itself an indication of the purpose for which it is to be used—they believed that *Lobaria pulmonaria*, which so closely resembles lung tissue, was good for diseases of the lungs; and that *Peltigera aphthosa*, with the little eruptions all over the thallus, was good for the thrush; and that *Xanthoria parietina*, that beautiful yellow lichen, was good for jaundice. To-day, however, Iceland Moss—*Cetraria islandica*—is perhaps the only lichen that still is used. It at one time had a prominent place in our Materia Medica, and was one of the articles in the U. S. Pharmacopoea even as late as 1900.

Due to the fact that nearly all lichens contain a bitter principle, most disagreeable to the taste, they are used as food only in countries where nothing else is likely to grow, and then only in case of famine. The "manna" which supplied the Children of Israel during their sojourn in the desert, is generally supposed to be a species of *Lecanora*—*L. esculenta*. This lichen, loosely attached, is carried by the wind quite readily, and in countries where it occurs plentifully, is sometimes brought in quantity from the mountain sides down into the valleys.

The only discovery of especial interest that was made in this long period (that is, from Aristotle to Tournefort), was that of Malpighi, who discovered the *soredia*<sup>3</sup>; he understood them to be propagative organs, and for that reason considered them true seed.

It was Tournefort (1694), who first considered the Lichens as a distinct class of plants; up to his time they were given no definite position in the vegetable kingdom, and were classified variously, as Algae, Fungi, Liverworts, and Mosses.

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<sup>3</sup>The little patches of powdery or mealy substance formed on the upper surface or margin of many lichens.

Between the time of Tournefort and Linnaeus, we still find that little progress has been made, notwithstanding that the Lichens were receiving a little more attention. Most investigators at this time were interested in the question if the Lichens had flowers, fruit and seed, as in the case of the Phanerogams, whether these parts could be seen or not; that is whether the parts observed on Lichens could be taken as such. Micheli, an Italian botanist, believed the soredia to be seeds, and the apothecium<sup>4</sup>, the calyx cup and floral receptacle. He also saw the spores, but took them to be buds.

Dillen an English botanist, at first, was going to throw all this aside but, nevertheless, later expressed himself thus: that the soredia were pollen grains, and the apothecia, seed vessels or the seed itself. Linnaeus believed the apothecia to be male organs, and the soredia female organs. Heller, one of the foremost lichenists of his time, and a cotemporary of Linnaeus, believed as Micheli; that is, that the soredia were seeds, and the apothecium a calyx cup.

It goes without saying, that most of these ideas were not founded upon direct observations, but were merely opinions.

As already stated, Linnaeus paid little attention to the Lichens; in his "Species Plantarum," he mentions 86 species, although 170 were known at the time.

The next 100 years was the era of the systematists, 1051 species of Lichens having been described as occurring in Germany and Switzerland alone. Discoveries concerning the nature of Lichens were very few, the chief of these being the following: (1) The discovery of the spermatogonia<sup>5</sup> by Hedwig (1784)—he believed them to be the male reproductive organs and the apothecia with their spores to be the female reproductive organs, and the soredia, a fertilizing element, or the true pollen. (2) The discovery of the gonidia<sup>6</sup> by Wallroth (1825), the most important discovery thus far made. He called them gonidia because of their resemblance to spores (γεννη, generation, εἶδος resemblance). He made a careful study of the soredia, and found that they consisted of gonidia enclosed by a delicate network (hyphae), and held the opinion, that the gonidia, therefore also the soredia, could develop into new plants. He believed that the gonidia and spores were the only reproductive organs of Lichens. His ideas concerning the gonidia received general recognition. Thus we read in Lindsay (A Popular History of British Lichens, 1856): "They (the gonidia) may be regarded as intermediate in function between the vegetative and reproductive cell, assuming the offices and partaking the characters of both. Their great peculiarity, is the want of union between each other and between them and surrounding tissues. They frequently break through the cortical layer, appearing on its surface in the form of powdery masses, denominated soredia." Lindsay, too, in speaking of the position of Lichens, says: ". . . by their reproductive system, Lichens are closely allied to the Fungi, by their vegetative system, to the Algae,

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<sup>4</sup>The fructification or spore-bearing structure of the lichen.

<sup>5</sup>Minute cup-shaped structures immersed in the upper surface of the thallus, appearing to the naked eye as minute black specks.

<sup>6</sup>The green cells, or Algae, found in the lichen-thallus.

from both they are distinguished by the presence of gonidia, as an essential element of their thallus."

The last statement gives us a pretty good idea of the notion as to what Lichens really were about the time when Schwendener presented his important discovery. At this time, all lichenists believed Lichens to be autonomous, co-equal in rank with Algae and Fungi. The gonidia, they believed, were peculiar cells formed right in the thallus of the Lichen. Schwendener, too, at first, firmly believed this; so we find him making the following statement in one of his "Untersuchungen über den Flechtenthallus;"<sup>7</sup> "The green cells or gonidia are, as all know, lateral formations of the hyphae, and as such are analogous to branches. Like the latter, . . . they never develop from apical cells, and in their early development can not be distinguished from them. The difference between the two shoots, however, soon becomes noticeable. While the branch by repeated division of cells, grows indefinitely in length, we find that in the formation of a gonidium, that the rule is, that the first cell divides once only, so that the branch becomes only two-celled. The apical cell now swells out spherically and becomes a gonidium, whilst the basal cell, does not change and becomes a sometimes longer sometimes shorter stalk. (Plate, I, Fig. 18.)" In a foot-note Schwendener adds: "That the gonidia develop from hyphae cells is a fact already discovered by Bährhoffer and verified by Speersneider and others. There really is no difficulty in convincing one's self through one's own investigations that they (the gonidia) are connected by short stalks to the hyphae." After describing how to proceed to see this, he adds: "Most of the gonidia, of course will be torn loose, nevertheless, some will be found, here and there, that will still be found in their original relationship with the hyphae." On page 126, he says: "Of especial importance to the plant is the multiplication of the gonidia, which occurs through division. The first plane of division, through which the spherical cell is divided into two hemispheres, lies in a plane passing through the point of attachment and the center of the green cell, in such a way that the stalk cell remains in connection with the two daughter cells."

This goes to show that Schwendener, at this time, was a firm believer in the prevailing notions regarding Lichens, and far behind DeBary, whom he soon was destined to outstrip.

It was DeBary who first hinted at the true nature of Lichens. In his "Morphology and Physiology of the Fungi, Lichens and Myxomycetes," he expresses the belief that some of the gelatinous Lichens (*Collema*ceae), were "either mature states of those plants, whose immature states are recognized as forms of *Nostoc*, *Chroococcus*, etc., or that these organisms are true Algae, attacked by some *Ascomycetes*, whose hyphae penetrate the Algae, and form the lichen-thallus."

In 1867 (published 1868), Schwendener expresses himself as of the same opinion as DeBary regarding the gelatinous Lichens. In the same paper, he further asks the question—if the gonidia of all Lichens are not Algae, and the hyphae, Fungus-hyphae. Schwendener's further investigations soon convinced

<sup>7</sup>Nageli. Beitrage II, p. 125.

him of the truth of the surmise, and in the same year, September, 1867, he presented his now famous talk "On true nature of Lichens" before the Swiss Naturalists' Club at Rheinfelden. The same was communicated by letter to DeBary, and was published by Von Mohl in 1868 in the *Botanische Zeitung*. Here he expresses the opinion that the gonidia of various Lichens correspond to certain low forms of Algae. His conclusions at that time, may be summarized as follows:<sup>8</sup> (1). There is no direct proof of any genetic relationship between the gonidia and the hyphal elements. (2) The cell-walls of the gonidia have a different chemical behavior from the membranes of the hyphae; the former react similarly to those of Algae; the latter similarly to those of Fungf. (3) As to structure and development, the various forms of gonidia correspond to different forms of Algae. The resemblance is so close that in many cases a given isolated gonidium cannot be distinguished from the corresponding Alga.

The next year 1869, he published his "Die Algentypen der Flechtengonidien". Here is what he says in his preface: "According to my investigations, these growths are not simple plants, not individuals in the ordinary sense of the word, they are more likely colonies, composed of hundreds and thousands of individuals. Of them, however, one only is in control, whilst the others, forever imprisoned, provide for themselves and their master, nourishment.

"This master is a fungus, of the class Ascomycetes, a parasite, accustomed to live upon the work of others, its slaves are green Algae, which it has gathered around itself, at any rate, holds on to and forces into service. It invests them as a spider her prey, with a fine meshed web, which gradually is converted into an impregnable integument, but, whilst the spider sucks out her prey and throws it aside when dead, the Fungus stimulates the Algae, found in its net, to more lively activity, in fact, causes them to grow larger and causes thereby a luxuriant growth and the thrifty appearance of the whole colony."

About the same time that Schwendener was making his investigations, two other botanists, Famintzin and Baranetsky were also working upon the development of the gonidia. These two investigators had succeeded in developing the gonidia of three different Lichens apart from their thallus, (*Xanthoria parietina*, *Evernia furfuracea*, and a *Cladonia*). They made the interesting discovery that many of these gonidia produced zoospores, whilst others dividing themselves in various ways, formed masses of cells which separated and rounded themselves; in fact, they concluded that the gonidia, thus capable of living apart, were identical with the Alga *Cystococcus*. They concluded from this that the forming of zoospores was not only peculiar to Algae and Fungi, but also to Lichens; furthermore, that *Cystococcus* was now no longer to be looked upon as an independent Alga, but one of the forms in the evolution of a Lichen, and that many more such forms would likely be discovered later and withdrawn from the Algae. They believed, therefore, that many of the unicellular Algae were merely free Lichen gonidia.

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<sup>8</sup>Schneider. A Text book of General Lichenology, page 24.

Now, up to this time, as all students of Lichens believed in their autonomy, one may readily surmise that Schwendener's advanced theory regarding them was likely to cause bitter controversy, and such it did. The systematists, with one accord, stood as one man against it.

Nylander, the greatest systematist of his day, came out at once against it, and seemed to favor Famintzin and Baranetzky. Krempelhuber, "Geschichte der Flechten," writing of the situation at the close of 1870, does not feel sure which theory is correct. He felt much concern that Sachs had sided with Schwendener. He feared that he might be promulgating an error and he thought that of the two theories Famintzin's was more plausible, and adds: "Even if Schwendener is right, it is questionable if one should classify the Lichens with Fungi, to do in other words, what the healthy mind finds unnatural and forced."

In 1874 Bornet, "Recherches sur les gonidies des lichens," isolated and determined specifically the Algae which enter into the composition of a large number of Lichens. The situation, however was not materially changed.

It is interesting, that the systematists, those who really, at any rate from their point of view, know the Lichens best of all, have always stood for the autonomy of Lichens. Nylander never was of any other opinion, and we find him writing thus in the preface of his "Les Lichens des Environs de Paris," 1896: "It is a true saying to-day that the formula 'Lichens are Fungi living in symbiosis with Algae,' is an assertion either of pure fantasy or a slander. It is fully proven that the Lichens constitute a noble and venerable autonomous class of plants having nothing seriously in common either with the Fungi or with the Algae. To subordinate the Lichens to the Fungi is even more absurd than to reunite the Characeae with the Algae. From the biological point of view the Lichens are sufficiently differentiated by the indefinite longevity which characterizes them. The beautiful specimens of *Umbilicaria pustulata* in the forest of Fontainebleau are probably a little less aged than the rocks upon which they display themselves," and, in a foot-note, "A new argument against the famous formula above mentioned is given by the volcanic peaks which raise themselves from the midst of the ocean, and which one finds covered with Lichens, the only plants which form themselves there first, it is the primordial vegetation. It is impossible to admit the intervention of a symbiosis whatever, in the multiplication of the saxicoline Lichens, since Algae and Fungi are absolutely lacking under these circumstances."

And Korber says: "The hyphae produced by the germination of a Lichen spore, must meet with the gonidia specifically belonging to it, that is coming from the particular Lichen species, if it is to give rise to a normal thallus. But the hyphae and whatever else there is in the Lichen thallus except the gonidia do not belong to a Fungus but to the Lichen, and the gonidia which are specifically necessary, are no Algae, but free independent Lichen gonidia, which have become asynthetic."<sup>9</sup>

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<sup>9</sup>DeBary. Comparative Morphology and Biology of the Fungi, Mycetozoa and Bacteria, 1887. page 418.

The view that the lower Algae, which vegetate where Lichens are found, are Lichen gonidia escaped from the thallus, originated with Wallroth, and was often expressed after him. There thus came to be two classes of followers: those who believed as Schwendener, and those who believed as Famintzin.

Up to this time, the experimental formation of a Lichen from its two components had not been accomplished, and, until this had been done, the question, of course, could not be considered settled. This was left to Stahl. Stahl's experiments, however, were not the first ones having this object in view. Already, in 1871, M. Reese had made the attempt, and he actually succeeded in forming a thallus, but he was not able to bring it to the formation of fruit and spores. In the same year Bornet repeated Reese's attempt, but with no better success. Treub, 1873, next tried, and again the results were no better than those of his predecessors. "This is, of course, what is to be expected," said those opposed to Schwendener. Hear what Crombie, England's great systematist, had to say upon the above experiments: "All these experiments, however, met with but a very limited amount of success, just as in the case of spore-culture by itself without any added 'algals.' Even where the spores successfully germinated and produced hyphae, all that could be affirmed was that these formed with the Algae a structure resembling in some degree the more or less rudimentary thallus of a Lichen. But it is to be observed with respect to these synthetical cultures, and all other experiments of a similar kind, that even were the results more pronounced than they have been, they would prove absolutely nothing as to the truth of the hypothesis. The Lichen-spore must, from its very nature, produce Lichen-hyphae, whether with or without the addition of algals or pseudo-algals; though what the fate of true added Algae in the subsequent evolution of the thallus might be, the experiments in *Symbiosis* do not show."<sup>13</sup>

Crombie, like Nylander, never believed otherwise, than that Lichens formed a distinct class of plants. In the article, from which the above is quoted, page 281, he says: "From all these various considerations and illustrations, to which others, though of minor importance, might easily be added, it is clear that the Algo-lichen hypothesis rests upon no solid basis whatever, but simply and solely upon imagination, and that it is merely a plausible attempt to explain certain phenomena which its author and adherents supposed to be otherwise inexplicable. Notwithstanding the laboured arguments by which it has been sought to deprive them of their autonomy and intrude them amongst the Ascomycetes, Lichens still remain a distinct class of plants, intermediate between the Algae and the Fungi, . . . . Lichens therefore are Lichens and nothing else —neither Fungi nor Algae, nor any intermixture of these: but everywhere and constantly preserving their own distinct type, and distinguished by many important characters peculiar to themselves."

It was in 1877 that Stahl succeeded in effecting the synthesis of three different species of Lichens. He did this by allowing the spores of the Lichens to ger-

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<sup>13</sup>Rev. J. M. Crombie. On the Algo-Lichen Hypothesis, Linn. Journ.-Botany, Vol. XXI. pag 266.



minate in contact with the hymenial algae that had been expelled with the spores and had stuck to them.<sup>11</sup> These and other experiments soon demonstrated beyond a doubt the dual nature of Lichens.

There arose, however, the question as to the nature of the relationship of the two components towards each other. Schwendener called it parasitism, and he and his followers uniformly agreed to classify Lichens as Fungi, to all of which, as already stated, the systematists objected very strongly. DeBary called the relationship symbiosis—a union for mutual good, enabling these plants to exist where neither of the components could exist alone—and this I believe is the prevailing view. Pfeffer, for example, in his "Physiology of Plants," Vol I, page 370, says: "Lichens are good examples of reciprocal symbiosis, for they are *specific* organisms formed by the union of a fungus and one or more algae, and can frequently withstand climatic conditions to which the isolated component parts succumb. The fungus, especially in those lichens which grow upon bare rocks, obtains organic food from the algae, while the fungal mycelium supplies the latter with water and salts, or even with proteids when the symbiotic algae are peptone-organisms." These views are, no doubt, all due to the influence of Reinke, the greatest of the upholders of the autonomous nature of Lichens. He calls the relationship of Fungus to Alga "consortism," and says: "We have, therefore, in the thallus of Lichens, a consortism, the components of which form a unit, a morphological individual, somewhat as the different tissues in a higher plant unite to form the individual. The fact that the alga can exist independently is dependent upon its ability to assimilate carbon. In the state of consortism, at least in the heteromercous thallus, the alga is nourished by the enclosing fungus, that is, it receives from the hyphae the necessary minerals, nitrogen, hydrogen and water. The alga in return supplies the fungus with the essential carbon compounds. From this it is evident that the components (Alga and Fungus) are biologically associated, mutually dependent upon each other for the formation of the organic substances required for the upbuilding of the common body."

However, the question does not seem to be any nearer solution to-day: each side has its followers. Several years ago, (1911) Professor Fink, of Miami, Ohio, wishing to get some sort of an idea how botanists, and especially lichenists, stood upon the question "Should the Lichens be maintained as a distinct class of plants or should they be distributed among the Fungi?"<sup>12</sup> . . . , wrote to 75 Americans and 75 Europeans. Of the 115 replies received, 19, or about 17%, favored distribution; 14, or about 12%, thought that Lichens might be distributed, but for one reason or other prefer that they should remain a distinct group. In other words, 83% of the 115, believe that Lichens should be maintained as a distinct group. A closer examination of the replies showed that the lichenists were nearly unanimously in favor of maintaining the group Lichens.

<sup>11</sup>Sahl. Beitrage zur Entwicklungsgeschichte der Flechten, II. Leipzig, 1877.

<sup>12</sup>Mycologia, September, 1911, and May, 1913.

Before bringing this paper to a close, a few words must be said on Stahl's discovery of the sexuality of Lichens. See his *Beitrage zur Entwicklungs-geschichte der Flechten*, 1877. The spermagones had been discovered for quite a while, and several investigators had already made extensive studies regarding them and their enclosed spermatia. Tulasne, 1852, for example, had studied them and believed that they were peculiar reproductive organs closely related to the apothecia. Lindsay also studied them, and was inclined to believe them male reproductive organs. Stahl now concludes that in *Collema*, one of the gelatinous Lichens, the spermatia are the male reproductive organs. The female reproductive organ he calls a carpogone. It consists of a spirally rolled portion, the ascogone, and a slender hyphal portion the trichogyne; the ascogone is inside the thallus some distance below its surface; the tip of the trichogyne penetrates the surface. Fertilization takes place by the spermatia coming in contact with the tip of the trichogyne, later resulting in the formation of an apothecium with asci and spores. Stahl's results have been verified and similar reproductive organs have been found in other species of Lichens. However, not all Lichens behave in this way, as many of them form their fruits apogamously; in fact, there are a number of different ways, many of the supposed apogamous Lichens, for example, are now believed to have internal trichogynes and internal spermatia. Then again some investigators have demonstrated that the spermatia will develop a hyphal net-work, even developing new spermatogonia, which would seem to show that the spermatia, in some cases, are true spores instead of sexual organs. As a matter of fact, our knowledge regarding the formation of reproductive organs, apothecia, and other structures is very meager, and many more investigations must be made before we can feel sure of the results.

3933 LOWNDES AVE., BALTIMORE, MD.

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**MOSES OF THE CASCADE MOUNTAINS, WASHINGTON**  
**COLLECTED BY J. A. ALLEN<sup>1</sup>**

M. E. SEYMOUR

The mosses collected in the vicinity of Mt. Rainier by J. A. Allen and his father were distributed in sets, several years ago. As there are still a number of these sets which have not been disposed of it may be well to put on record the names of the mosses as they are a very fine set of specimens, in good fruiting condition, and include some rare or unusual species.

*Alsia abietina*, *Amphidium lapponicum*, *Antitrichia californica*, *A. curtispendula*, var. *gigantea*.

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<sup>1</sup>The names used in this article are those under which the mosses were distributed, thus differing in some instances from present usage.

- line 28, for *Muhlenbeckii* read *Muhlenbergii*.
- line 3 from bottom, for Sulliv. read (Sulliv.) Grout.
- bottom line, for Lindb. read (Lindb.) Correns.
- Page 26, line 9, for B. & S. read R. & C.
- line 18, for Pers. read Crome.
- line 24, for B. & S. read Lindb.
- line 26, for *americana* read *americanum*.
- Page 52, fifth line from bottom, for *thelistegium* read *thelistegum*.
- Page 74, line 14, for *osmundaceae* read *osmundacea*.
- Page 81, line 10, for Fungf. read Fungi.
- Page 86, line 17, for *Heterocladium* read *Heterocladium*.
- Page 86, line 7 from bottom, for *vancourveriense* read *vancouveriense*.